HENDRICHS, H., und HENDRICHS, U. (1971): Dikdik und Elefanten. Ökologie und Soziologie zweier afrikanischer Huftiere. R. Piper & Co, München.

KÜHNEL, W. (1971): Die Glandulae rectales (Proctodaealdrüsen) beim Kaninchen. Lichtmikroskopische und histochemische Untersuchungen. Z. Zellf. 118, 127—141.

Montagna, W. (1962): The structure and function of skin. Second edition, Academic Press New York.

MÜLLER-SCHWARZE, D., und LEMPERLE, E. (1964): Objektivierung und Analyse olfaktorischer Signale der Säugetiere mit Hilfe der Gaschromatographie. Die Naturwiss. 51, 346—347.

MUNGER, B. L. (1965 a): The Cytology of apocrine sweat glands. I. Cat and Monkey. Z. Zellf. 67, 373—389.

- (1965 b): The Cytology of apocrine sweat glands. II. Human. Z. Zellf. 68, 837—851.

Рососк, R. J. (1910): On the specialised cutaneous glands of Ruminants. Proc. Zool. Soc. London, 840—896.

 (1918): On some external characters of Ruminant Artiodactyla. Part I. The Cephalophinae, Oreotraginae and Madoquinae. Ann. Mag. Nat. Hist. Vol. I (9. Ser.), 426—436.

Ruprecht, K. W. (1971): Pigmentierung der Dunenfeder von Gallus domesticus L. Z. Zellf. 112, 396-413.

Schaffer, J. (1923): Neue Drüsentypen. Verh. Anat. Ges. 32. Vers. Heidelberg, 242-252.

- (1924): Zur Einteilung der Hautdrüsen. Anat. Anz. 57, 353-372.

(1940): Die Hautdrüsenorgane der Säugetiere mit besonderer Berücksichtigung ihres histologischen Aufbaues und Bemerkungen über die Proktodäaldrüsen. Urban & Schwarzenberg, Berlin und Wien.

Schiefferdecker, P. (1917, 1922): Die Hautdrüsen des Menschen und der Säugetiere, ihre biologische und rassenanatomische Bedeutung, sowie die Muscularis sexualis. Biol. Zentralbl. 37 (1917) 534—562 (vorl. Mitteilung) und Zoologica 27 (Heft 72) (1922) 1—154.

SCHUMACHER, S. v. (1917): Eine "Pigmentdrüse" in der Nasenhaut des Hasen. Anat. Anz. 50,

161—171.

SIMONETTA, A. M. (1966): Osservazioni etologiche ed ecologiche sui Dik-Dik (gen. Madoqua; Mammalia, Bovidae) in Somalia. Mon. Zool. Ital. 74, Suppl., 1—33.
 STARCK, D. (1964): Herkunft und Entwicklung der Pigmentzellen. In Japasson, J.: Handbuch

STARCK, D. (1964): Herkunft und Entwicklung der Pigmentzellen. In JADASSON, J.: Handbuch der Haut- und Geschlechtskrankheiten, Bd. I, Teil II, p. 139—175, Springer, Berlin — Göttingen — Heidelberg — New York.

STARCK, D., und SCHNEIDER, R. (1971): Zur Kenntnis insbesondere der Hautdrüsen von Pelea capreolus (Artiodactyla, Bovidae, Antilopinae, Peleini). Z. Säugetierkunde 36, 321 bis 342.

Tinley, K. L. (1969): Dikdik *Madoqua kirki* in South West Afrika: Notes on Distribution, Ecology and Behaviour. Madoqua 1, 7—33.

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An Analysis of the Mechanisms of Brooming of Mountain Sheep Horns

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Introduction

In many species of mountain sheep (Ovis) the horns are found to suffer some form of damage. Most frequently the tips are broken or splintered. In North American sheep, horns which exhibit this type of damage are said to be "broomed". Brooming

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is usually observed in rams with horns of greater than 3/4 curl. Despite a noticeable variation in the degree of brooming, between conspecifics certain species appear to be more susceptible to the phenomenon than others. A number of hypotheses have been proposed to account for its occurrence, and some of the more plausible ones will be examined below.

OBER (1931; cited in COWAN 1940) suggested that the horn tips became broken or worn as a result of the rams using their horns to dig for food. Our behavioural observations do not support this idea, nor have any such observations been *eported in the literature. Although sheep will dig for certain foods items, they do so using only their front feet or occasionally the nose.

A popular belief holds that a ram's horns on attaining a certain length interfere with his vision, and that it then rubs away the offending portion. The nature and variety of the broken tips could not be the result of this activity alone as we will explain below. Rams have not been observed to rub or horn for long periods of time, as one would expect from the degree to which the horns of some individuals are broomed. Also, many rams are observed with heavy brooming although the tips are still on or above eye level and could still theoretically interfere with vision.

SHELDON (cited in COWAN 1940) suggested that the horns of rams were damaged during fights between males. This conclusion was also reached by several other authors (Welles and Welles 1961, Egorov 1965, Geist 1966, 1971). Geist (1971) described chips of the horn from the basal region broken off during fighting and also illustrated splintered horn tips resulting from combat. However, none of these authors explored the mechanisms responsible for brooming.

The purpose of this present paper is to provide evidence for the possible mechanism involved in brooming, and for the variability of this phenomenon observed both between individuals and between species.

Results and Discussion

Morphology of broomed horns

A large number of horns were examined from skulls and on live rams, belonging to a population of Rocky Mountain bighorn sheep (Ovis canadensis canadensis Shaw), inhabiting the Cascade Valley, Banff National Park, Alberta. Variability of the structure of the broomed tips was found to be considerable. However, when the various types were viewed together they suggested a developmental series of brooming stages (Fig. 1). It was found that, within certain limits the older the ram and the longer its horns, the more extensive was the degree of brooming.

In young males with horns of approximately ³/₄ curl or greater brooming became first evident in the form of a split at the terminal region of the horn (Fig. 1 A). These splits were found invariably to run from the tip to the outer edge of the horn, appearing to be caused by a force or blow exerted on the tip and directed away from the centre of the horn curl.

Further brooming was found to result in fraying and shattering of the tip (Fig. 1B), and was followed by a flattened and crushed tip (Fig. 1C). This latter type would suggest a blow aimed directly at the horn tip to produce the flattening and crushed appearance. The next stage was a secondary splitting of the outer edge of the tip face (Fig. 1D)). The blow responsible for this type of damage would have to have struck the flattened face just off centre and towards the outer edge, and again be directed away from the centre of the horn curl. Finally, in those rams with exceptional horn development, the damage was no longer concentrated at the tip itself, but at the outer

edge of the distal end of the horn. The normally rugose surface of the horn in this region now appears smooth and somewhat polished (Fig. 1E).

The fact that these different types of broomed tips formed a developmental series of brooming stages was suggested not only by the differing degree of these brooming stages and their direct relationship to horn length, but also by the fact that in certain

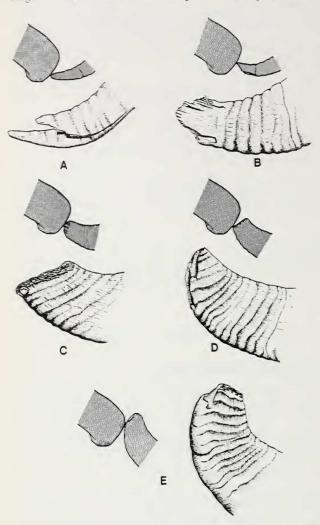


Fig. 1. Variation and development of broomed horn tips of bighorn sheep (Oxis canadensis canadensis). Upper left shaded diagrams show blow experienced by horn tip from horn base of opponent during a clash. A: Horn tip of a 3.4 curl, 5-year old ram showing first signs of brooming; B: Horn tip of greater than 3.4 curl, 7-year old ram; C: Flattened and crushed tip of horn from 4.5 curl ram, aged 8½-years; D: Secondary splitting of horn tip, with retainment of crushed surface as in C. of almost full curl ram 10-years old; E: Horn tip of full curl, 13-year old ram, showing smooth outer edge, also secondary split as in D and crushed surface as in C. (All illustrations of horn tips taken from photographs)

stages characters of preceding stages could be readily detected. Comparison of the structures of the horn tips illustrated in figures 1 C, D and E show that the flattened and crushed tips of 1 C is present in the latter two stages, although they also show a greater degree of brooming.

Clash posture and its relationship to brooming

The fighting behaviour of male bighorn sheep has been described in detail by GEIST (1966 bis 1971). It was found that when two rams clashed they invariably twisted their heads and horns as illustrated in figures 2 and 4. The result of this orientation of the horns during a clash is to bring the tip of the raised horn of a ram into close proximity with the basal region of the lowered horn of his opponement (Figs. 3, 4). This would not be the case if the rams clashed directly with no twisting of the heads.

We suggest that this orientation of the horns by fighting rams frequently results in the forceful contact of an opponent's horn base with the horn tip of the other ram, and that this is the mechanism which results



Fig. 2. Clash posture of bighorn rams, illustrating twisted orientation of horns and heads at impact

in the majority of observed brooming. From this hypothesis we should expect that the postulated mechanism will account for the observed variability and apparent sequential development of brooming.

It was previously noted that rams usually begin to broom when the horns exceed the 3/4 curl. At this time the brooming is characterized by a single split at the tip which eventually becomes complete and the terminal portion detached and lost. The direction of the split running from the tip to the outer edge of the horn could only suggest a blow directed away from the centre of the horn curl, which would be provided by the blow experienced from the horn base of an opponent falling on the inner side of the horn tip. (Fig. 1 A.).

Further development of brooming was suggested to be dependent upon a change in the orientation of the blow in relation to the horn tip. In fact the postulated mechanism would suggest that it was not the blow which changed but rather the orientation of the tip itself, which would have the same result. Despite the shortening effect of brooming, horns continue to increase in length with subsequent growth. This increase in the length of the horn will alter the orientation of the tip to an opponent's horn base during a clash. This change in tip orientation is illustrated in the series of figures, IA — E.

Welles and Welles (1961) suggested that brooming occurred from blows received during "Miss-fire" clashes, when rams failed to catch each others blows correctly. Undoubtedly some damage does occur under these circumstances, as such atypical clashes are not uncommon. However, the somewhat random nature of these blows could not be expected to produce the types of broomed tips which we observed, nor



Fig. 3. Moment of impact during a clash between bighorn rams showing contact between the horn tip of one ram and the horn base of the opponent

their sequential relationship. For example, in the early stages of brooming the direction of the first split is to the outer edge of the horn, produced by a blow directed to the inner edge of the tip away from the centre of the horn curl. The type of blow most likely to be received in a "Miss-fire" clash would be received on the outer edge of the horn tip forcing it in towards the centre of the horn curl. Thus the resulting split would run from the outer edge towards the tip of the horn, quite the converse of what we observed.

It may be further suggested that the horning activity of rams, when the animal pushes and twists its horns against some object such as the ground or a tree, could affect the tips of the horns, especially in rams with complete or greater curled horns (Fig. 5). Horning was observed in rams of all ages and the activity was directed

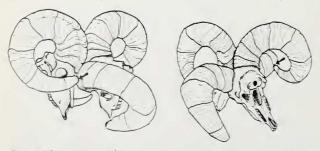


Fig. 4. The moment of impact illustrated by placing two skulls of bighorn rams in the cash posture. Left hand figure as in Fig. 3, right hand pair as in Fig. 2. (Taken from photographs)

towards the bases of the horns rather than at the tips. In the case of full curl rams the tips would also be in contact with the substrate, and if the tips are being abraded by this behaviour we should also find similar wear on the frontal regions of the horn bases. This we did not observe, and can only conclude that any effect

on the horn tips from horning behaviour must be negligible.

Intra- and Interspecific variation of brooming

Broomed horns were rarely found in rams with horns describing less than a ³/₄ curl. When the horns exceeded this size the tips became projected far enough forward to be contacted by an opponent's horn during a clash. From our observations it was apparent

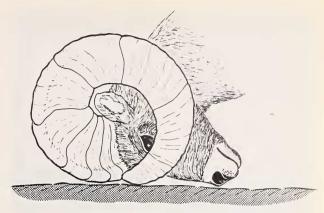


Fig. 5. Relationship of horn bases and horn tips to substrate, in bighorn ram engaged in horning behaviour

that the attainment of this stage of horn development, besides being a function of horn length and age, was also dependant upon two other horn characteristics; the diameter of the circle described by the horns (i. e. tightness of curl), and the degree of divergence of the horn tips from the skull.

The diameter of the horn curl will naturally determine, within certain limits, the age and horn length at which brooming will begin. The tips of the horns describing relatively small circles will exceed the ³/₄ stage, and hence allow brooming, at an earlier age and shorter horn length than similar aged rams with more open curls. It is also likely, though we have no observations to support this, that if a ram had horns with exceptionally small horn curls, brooming would be unlikely to occur or only at a very advanced age.

A measure of the degree of divergence of the horns from the head is for most purposes provided by the distance between the horn tips, i. e. horn spread. Rams with very wide spread horns were found to show less brooming than similar aged animals with relatively narrow spread horns. Reference to Fig. 3, will show that any increase in the horn spread of one of the rams would reduce the probability that its horn tip would contact its opponent's horn. This would also hold for rams whose horn tips, rather than the horns themselves, are extremely flaired, and of course the reverse in rams with inward directed tips though the horns may otherwise be regarded as being wide spread.

Combinations of these two characters will result in the great variability in the degree of brooming between similar aged rams of the same population or species. We also observed variation between the two horns of an individual. A number of rams were observed in which one horn was broomed more than the other. Closer examination of the horns revealed asymmetrical horn development (Fig. 6). The asymmetry was found to be in the differing degrees of divergence of each horn from the skull, with the wider spread horn showing less brooming; or the curls of the horns had different diameters such that the horn with the smaller diameter curl had been broomed to a greater degree. However, there were a number of skulls of younger rams in which brooming was just beginning, but only on one horn. In these specimens we could find no evidence of asymmetrical horn development. Geist (1971) found that the young and therefore (usually) subordinate rams initiated a clash. They should therefore have the prerogative to determine in which direction they will twist their head. The opponent, the older and dominant ram, would have to orientate his head



Fig. 6. Bighorn ram with asymmetrical horn development and brooming. Right hand horn is more tightly curled, smaller and broomed to a greater degree than the more open curl of the left hand horn

according to this choice. Young rams will not only have had relatively few fights since attaining a horn length susceptible to brooming, but they may also be found to favour one direction in which to twist the horns during a clash when they have the choice, analogous to left or right-handedness.

Interspecific variation will parallel that found within a species and be dependant for its expression upon the species specific characteristics of horn configuration. Obviously in those species of mountain sheep with

heteronym horns (after Zalkin; in Pfeffer 1967) there will be no possibility for brooming to occur because of the backwardly directed horn tips. Any instances of damage will be extremely rare and must be the result of atypical clashes.

Among the species of mountain sheep with homonym and plane horn types, it is generally recognized that members of the species O. canadensis canadensis exhibit the greatest degree and frequency of brooming (Cowan 1940, Clark 1964). Adequate data is available only for 3 races of North American sheep, but it supports the observations of Cowan (1940) and Clarke (1964) that canadensis have the least divergent horns and the smallest diameter horn curls. It is possible that other species of mountain sheep clash differently from canadensis males, but reported observations of fighting behaviour of, O. dalli dalli, O. d. stonei (Geist 1966, 1971); O. c. nelsoni (Welles and Welles 1961); O. ammon (Walther 1961), and O. a. musimon (Pfeffer 1967), show that in all these species the rams twist their horns in a similar manner.

In those species with wide flaring horns such as O. dalli or O. a. poli, little brooming would be expected, nor is it frequently observed in any degree. CLARK (1964) observed that in O. a. poli there was little sign of brooming of their extremely long and spiralled horns, which we would expect from their great spread between the tips. However, he did find a number of rams which had suffered severe horn damage in the form of breaks close to the tips of the horn cores. In light of this preceding discussion, it is apparent that such damage must be received in atypical or "miss-fire" clashes, when the horn between the tip and the base receives a direct hit from an opponent. It would be highly unlikely that breaks of this nature would occur frequently as the resulting deformity would be highly deleterious to a ram, either in further social situation, or to its health (GEIST 1971). It is interesting to note that the short horned, tight-curled species O. a. hodgsoni show brooming as in bighorn sheep (see CLARK 1964).

We conclude therefore that the majority of horn damage observed in mountain sheep, particularly the type referred to as brooming, is received during fights between males as was suggested by previous authors. The mechanism which we have described and discussed accounts for the occurence of brooming, its sequential development, and the observed variability between individuals and between species. Although other behaviours may modify these effects, they could not alone account for either the high frequency of occurrence, or the degree to which mountain sheep horn become broomed.

Acknowledgements

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Summary

Damage to the horns, commonly referred to as brooming, is observed in many species of mountain sheep. The various hypotheses proposed to account for this phenomenon were examined in light of observations made on bighorn sheep (Ovis canadensis canadensis).

1. Behavioural observations do not support the suggestion that brooming resulted from the use of horns for digging for food.

2. The variety and nature of broomed horns, together with the lack of observations show that rams do not consciously abrade or damage the horn tips in order to restore full vision.

3. Examination of the broomed horns of mountain sheep suggest a developmental series of brooming stages.

4. Examination of the fighting mechanisms in mountain sheep support the original hypothesis of Sheldon that brooming occurs during fights between male sheep.

5. The orientation of the horns of rams during fights is such that the horn tips contact the opponent's horn base and this occurs frequently enough to account for both the high frequency and variety of broomed horns.

6. Brooming usually begins when a ram's horns form a 3/4 curl or greater.

7. Variation in the degree of brooming is the result of differences in horn conformation between individuals. Asymmetrical growth also affects the degree of brooming between two horns of an individual.

8. Interspecific variation in brooming is dependant upon species specific characteristics of

horn development and structure.

Zusammenfassung

In mehreren Wildschafarten findet man bei Böcken stark beschädigte Hornenden. Es werden verschiedene Erklärungen dieser Beschädigungen an Hand von Beobachtungen an Dickhornschafen (Ovis canadensis canadensis) überprüft.

1. Unsere Beobachtungen bestätigten nicht, daß die Hornenden durch Graben nach Asung abgenutzt werden. (Asung wird mit Hufen, nicht mit dem Gehörn, von Schnee freigescharrt).

2. Es konnte nicht festgestellt werden, daß Böcke die Hornenden abreiben um ein besseres Blickfeld zu erhalten.

3. Die Beschädigungen konnten in einer Serie steigender Intensität aufgereit werden.

- 4. Beobachtungen am Kampfverhalten zeigten, daß die Hornenden im Kampf beschädigt werden.
- 5. Während des Zusammenstoßes der Gehörne prallen die Hornenden des einen Kämpfers auf der Basis des Gehörnes des anderen auf. Dieses kommt häufig vor und erklärt die hohe Frequenz und die Art der Hornbeschädigungen.

6. Die Hornenden werden erst beschädigt, wenn das Gehörn einen dreiviertel Kreis geformt

7. Unterschiede in der Art der Hornbeschädigungen entstehen durch unterschiedlich geformte Hörner. Asymmetrisch geformte Gehörne führen zu unterschiedlichen Beschädigungen der Hornenden.

8. Intraspezifische Unterschiede in der Beschädigung der Hornenden können auf unterschied-

liche Ĥornstruktur zurückgeführt werden.

Literature

BAKER, L. R., and Bradley, W. G. (1965): Skull measurements of desert bighorn sheep from the Desert Game Range. Desert Bighorn Council Trans. IX, 70—74.

CLARK, J. L. (1964): The great arc of the wild sheep. Univ. of Oklahoma Press, Norma, xxxvi,

247 pp.

COWAN, I. McT. (1940): Distribution and variation in the native sheep of North America.

Amer. Midl. Nat. 24, 505—580.

EGOROV, O. V. (1965): Wild ungulates of Yakutia. Izdatel'stvo "Nauka", Moscova. (Translation: Israel Program for Scientific Translations, Jerusalem, 1967). 230 pp.

GEIST, V. (1966): On the behaviour and evolution of American mountain sheep. Unpubl. Ph. D. Thesis, Univ. of British Columbia. 252 pp.

- (1971): Mountain sheep: a study in behaviour and evolution. Univ. of Chicago Press. OBER, E. H. (1931): The mountain sheep of California. Calif. Fish and Game 17, 27—39. PFEFFER, P. (1967): Le Mouflon de Corse (Ovis ammon musimon Selveber 1782); Psition systematique, Ecologie et Ethologie comparees. Mammalia 31 (supplement), 262 pp.

WALTHER, F. (1961): Einige Verhaltensbeobachtungen am Bergwild des Georg-von-Opel-Frei-

geheges. G.-v.-Opel-Freigehege, Kronberg Jahrbuch, 53—89. Welles, R. E., and Welles, F. B. (1961): The bighorn of Death Valley. Fauna of the National Parks of the United States. Fauna Series No. 6, 242 pp.

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Über Schwingungsmessungen am Skelett des Mittelohres von Halicore (Sirenia)

Von GERALD FLEISCHER

Eingang des Ms. 9. 9. 1971

Problemstellung

Die Physiologie des Mittelohres der Säugetiere bereitet noch größere Schwierigkeiten, vor allem bei den aquatilen Arten. Meist wird angenommen, daß das Mittelohr allgemein nur die tieferen Frequenzen überträgt und daß darüber die Übertragung mittels der Knochenleitung erfolgt, also unter Umgehung des Mittelohres. Aus Messungen und theoretischen Überlegungen wird geschlossen, daß große und schwere Ossicula audita hochfrequenten Schwingungen nicht zu folgen vermögen. Die bekannte Tatsache, daß bei den Cetacea der Malleus fest mit dem Tympanicum verwachsen ist, wird so gedeutet, daß darin eine vollkommene oder doch weitgehende Funktionslosigkeit dieser Teile zum Ausdruck kommt.

Die Auffassung über das Dominieren der Knochenleitung bei wasserlebenden Säugetieren findet Schwierigkeiten bei der Erklärung der Tatsache, daß bei den allermeisten aquatischen Säugern das Perioticum (welches die Schallwellen aufnehmen soll) weitgehend, oder, wie bei den Cetacea und Sirenia, völlig akustisch vom übrigen Schädel-Skelett isoliert ist, was zu einer Herabsetzung der Fähigkeiten der Knochenleitung führt. Die gegenteilige Auffassung, daß nämlich die Schallaufnahme auch bei hohen und höchsten Frequenzen durch das Mittelohr erfolgt, wird gestützt durch eben diese akustische Isolierung, die theoretisch zu einem besseren Richtungshören führen muß und gleichzeitig wahrscheinlich macht, daß das Mittelohr die Weiterleitung von Schallreizen zum Innenohr übernimmt.1

¹ Eine ausführliche Diskussion dieser Probleme findet man bei Reysenbach de Haan (1957), sowie bei Dudock van Heel (1962), Fraser and Purves (1954, 1960), Purves (1966). Experimente sind zudem bei Mc Cormick et al. (1970) Møhl (1964, 1968) sowie Wever et al. (1948) auch theoretisch besprochen.

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